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Phenological, ecological, and demographic data of the slow worm (*Anguis fragilis*) population from southern Catalonia (Spain)

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Abstract

Studies on the slow worm (*Anguis fragilis*) in the Iberian Peninsula have primarily focused on northern and north-western populations, with limited data, based mainly on distribution short notes, on the north-eastern populations in Spain. This study examines the ecology, demography, and phenology of a slow worm population located at a suboptimal site near the southern edge of its distribution range on the Iberian Peninsula, characterized by a Mediterranean climate, in southwestern Europe. The study area encompasses 2.9 hectares in Tarragona Province, Spain, at an altitude of 990 m. Sixteen sampling stations were established to cover all available habitats. In this population, adults comprised 73.73% (n = 87) of individuals, with a sex ratio (♂♂/♂♂+♀♀) of 0.44. Of the captured individuals, 46.61% (n = 55) exhibited non-intact tails. The estimated apparent survival probabilities during the study period (1.5 years) were 0.76 (0.54, 0.94) for immatures, 0.79 (0.29, 0.95) for males, and 0.83 (0.68, 0.96) for females. Population density was estimated at 16.11 ind./ha (7.78, 45.42) for immatures, 44.39 ind./ha (30.38, 72.57) for males, and 64.08 ind./ha (35.35, 129.93) for females. The activity period extends from March to October, with males emerging from hibernation earlier than females, peaking in May. Female emergence occurs one month later, peaking in June. A total of 41.18% of captured males had recent scars and wounds, indicative of fighting during the mating season from mid-April to mid-June. Pregnant females were observed from mid-May to early September, with a peak incidence in June, which is an extended period compared to other European populations at similar altitudes and latitudes.

Key Words

activity cycle, Anguidae, biometry, demography, phenology, population size

Introduction

The slow worm (*Anguis fragilis*) is a lizard with a wide distribution throughout Europe (Strzała et al. 2017; Jablonski et al. 2021). The genus *Anguis* comprises five species: *Anguis fragilis*, *A. veronensis*, *A. cephallonica*, *A. colchica*, and *A. graeca* (Jablonski et al. 2021), previously considered *A. fragilis* (Salvador 1997).

In the Iberian Peninsula, *A. fragilis* is distributed in the northern half, with high abundance in the Cantabrian-Pyrenean strip. It becomes increasingly rare in more southern latitudes, with the populations of the lower Tajo basin in Portugal being the most southern known (Galán 2008; Jablonski et al. 2021). In the northeastern Iberian Peninsula, *A. fragilis* is restricted to Catalonia, where it is abundant in the northern third. From there,

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the distribution of the species decreases towards the south and west, where it is mainly confined to humid or mountain habitats. The southernmost known populations are located in the Montsant massif in the province of Tarragona (Soler-Massana et al. 2006). However, records of the species in the Ebro Delta confirm the existence of isolated populations further south along the Ebro River, specifically restricted to hygrophilous vegetation habitats within riparian forests (Roig 2008).

Studies on its spatial distribution and reproductive ecology have been published in several European countries outside the Iberian Peninsula (Stumpel 1985; Smith 1990; Platenberg 1999; Ceirans 2004; Brown and Roberts 2008; Haley 2014). Published studies about *A. fragilis* from northeastern Italy (Capula et al. 1992, 1998; Luiselli 1992; Capula and Luiselli 1993) could really be *A. veronensis*, according to Jablonski et al. (2016, 2021) and Gvoždík et al. (2013). According to these authors, the distribution limits of *A. veronensis* and the areas where it overlaps with *A. fragilis* remain poorly understood in the western part of their range (Gvoždík et al. 2013; Renet et al. 2018; Jablonski et al. 2021). Despite this, due to the lack of conclusive evidence, the slow worm from northeastern Italy is included in studies as *A. fragilis* (Mezzasalma et al. 2013).

Several studies have been published on the slow worm in Spain, including works by Braña (1982), Cabido et al. (2004), Ferreiro et al. (2007), Ferreiro and Galán (2004), and Galán and Fernández (1993). These studies have focused on populations in the north and northwest of the Iberian Peninsula. However, there is a lack of published data on the biology, demography, and ecology of *A. fragilis* from the northeastern populations of the Iberian Peninsula. This is probably due to the lack of optimal study areas, populations with generally low numbers of individuals, the scarcity of optimally known populations, and the difficulty of monitoring species with fossorial habits. The climatic factor may also be significant, as the Mediterranean climate has much lower humidity levels, making the area generally sub-optimal for the species.

This study aims to describe the ecology, demography, and phenology of one population of slow worms located in the province of Tarragona, in the southern distribution of the northeastern Iberian Peninsula.

Methods

Study area

The study area is 2.9 ha of plain located within the "Muntanyes ENP de Prades" (Tarragona, Spain) at an altitude of 990 m. The climate in the study area is oro-mediterranean, with cold winters and dry summers. The average annual rainfall in the area is 600–800 mm. It has a high diversity of mosaic habitats (Fig. 1), characterized by the dominance of a wet grassland of mosaic grasses with water points, numerous ground-level shelters, stone walls, and shrubby margins. The surrounding forest is dominated by *Pinus sylvestris*, *Pinus nigra*, and *Cedrus atlantica*, the latter two being

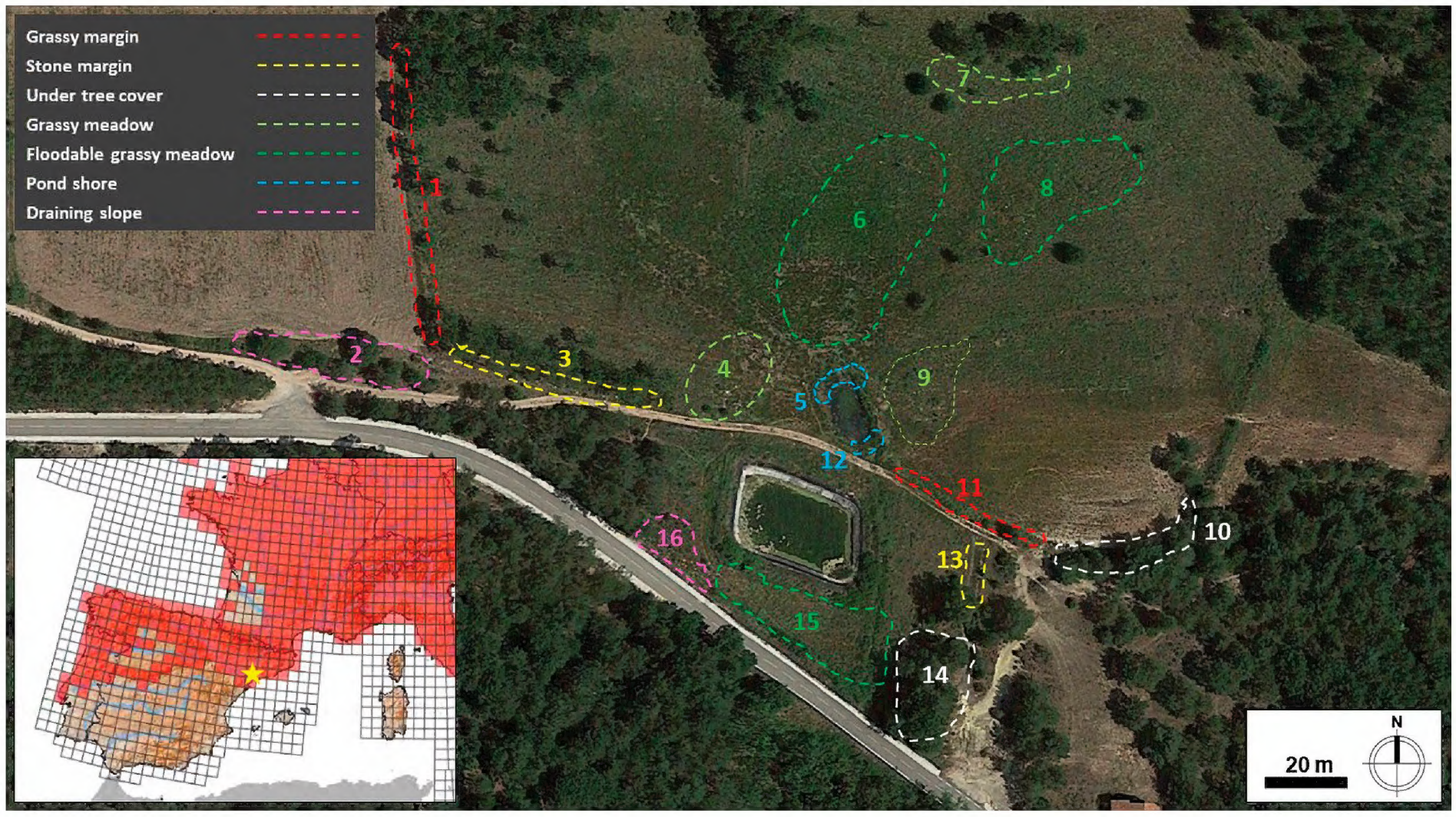

Figure 1. Study area and location of sampling stations: (1, and 11): grassy margin; (2, and 16): draining slope; (3, and 13): stony margin; (4, 7, and 9): grassy meadow; (6, 8, and 15): flooded grassy meadow; (10, and 14): stony margin under tree cover and *Pinus nigra* pine forest; (5, and 12): Pond shore. Low-left map, western distribution in Europe of *Anguis fragilis* (Sillero et al. 2014) with the studied population (yellow star).

non-autochthonous species introduced as a result of various reforestation actions carried out in the area in the 1980s. The central zone consists mainly of meadows that are prone to flooding. Two sub-zones can be distinguished: a floodable zone with a majority presence of *Brachypodium sp.* and *Juncus acutus*, and another one with isolated low and medium-sized shrubs of *Prunus spinosa*, *Crataegus monogyna*, *Juniperus oxycedrus*, *Buxus sempervirens*, and *Rubus caseius*.

The herpetological community includes the following species: *Salamandra salamandra* (Linnaeus, 1758), *Alytes obstetricans* (Laurenti, 1768), *Bufo spinosus* Daudin, 1803, *Epidalea calamita* (Laurenti, 1768), *Pelodytes punctatus* (Daudin, 1802), *Pelophylax perezi* (Seoane, 1885), *Psammodromus algirus* (Linnaeus, 1758), *Podarcis liolepis* (Boulenger, 1905), *Timon lepidus* (Daudin, 1802), *Chalcides striatus* (Cuvier, 1829), *Malpolon monspessulanus* (Hermann, 1804), *Coronella girondica* (Daudin, 1803), *Zamenis scalaris* (Schinz, 1822), *Natrix maura* (Linnaeus, 1758), *Natrix astreptophora* (Seoane, 1884) and *Vipera latastei* (Boscá, 1878) (García-Salmeron et al. 2023; Montori et al. 2024). The grasslands were grazed until recently. Without livestock control, the vegetation has become luxuriant. The human presence in this area is minimal.

In the study area, 16 sampling stations were determined to cover all available habitats and microhabitats (Fig. 1). These stations were situated in areas with concentrations of refugees, primarily characterized by scattered or stacked stones and logs naturally occurring within the study zone. During each visit, a total of 182 shelters were checked, with varying numbers at each station.

Sampling methodology

A systematic sampling of the delimited area was conducted, checking all the shelters at each sampling station. Sampling occurred fortnightly from March 2, 2015, to October 28, 2016, under favorable weather conditions. Sampling was interrupted from November 2015 to February 2016 due to the winter rest period of the species in the area (Roig, Giner, and Gómez, own data). Individuals were captured manually during the period when the animals were concluding their daily activity and settling in their shelters, approximately one hour before and after sunset. The sampling stations and the spatial locations (UTM 31N - ETRS89) of each individual were georeferenced using the HandyMobile GPS App with an accuracy of one meter. The animals were handled using gloves.

The following variables were recorded for each captured individual: sex (when showing secondary sexual characters such as body size, head shape, and coloration), stage (size classes: adult, subadult, and juvenile), weight (with a precision of 0.01 g), snout-vent length (SVL, with a precision of 1.00 mm), and tail length (TL, with a precision of 1.00 mm), recording whether the tail was regenerated or autotomized. Captured individuals with non-intact tails were considered invalid for general biometric studies, except for SVL. Females showing any signs of pregnancy were excluded from the average weight calculation, as they do not represent the average condition of the species.

The size classes were determined according to the criteria of Platenberg (1999), which are based on a stage of growth and maturation that is necessary for reproductive success. Individuals are considered adults when their SVL exceeds 130.00 mm. Those with a SVL below 100.00 mm were classified as juveniles, and those with a SVL between 100 and 130 mm were classified as subadults. In some cases, sexual maturity could not be clearly determined due to inconclusive coloration patterns or the absence of hemipene evagination.

The individuals were initially examined visually for combat marks in males, which could present characteristic markings, with particular attention paid to the size and shape of the jaws of *A. fragilis* on any part of the body. Additionally, pregnancy or copulation marks in females were identified. Copulation marks consist of scale scratches on the neck and head caused by the biting of males during copulation (Rollinat 1934). Finally, the identification of recaptures was also carried out. They were marked using a low-temperature electric cautery (model FIAB7255), commonly used in medical and veterinary practice and previously employed in studies by Ferreiro et al. (2004, 2007). A mark (individual identification code) was assigned to different body marks and dorsal body positions during the marking process, following techniques described by Ferreiro et al. (2007), Ferreiro and Galán (2004), and Stumpel (1985). Subsequently, the marked area was treated with an antiseptic iodine solution. After confirming the animal's condition, it was released back into the same shelter where it was initially captured. Neonates or individuals in very early stages were not marked due to their small size, resulting in most of them (n=18) being excluded from this aspect of the study. No complications arising from the marking method were observed in any of the recaptured animals. The marks remained visible throughout the follow-up period, even up to one year later. The sex ratio was estimated as the proportion of mature males to total adults (Wilson and Hardy 2009).

Data analysis

The population parameters were estimated using the POPAN model estimator, which is an adaptation of the Jolly-Seber model in terms of a superpopulation. The MARK™ software was used (Schwarz and Arnason 1996; White et al. 1999). The POPAN model assumes that the catchability of marked and unmarked individuals is the same, which we accept as true. Once all the models were obtained, the model with the lowest Akaike value (AICc) was selected as it is more robust and has a better fit to the data. The general model is as follows: POPAN - $p(g^*t)$, ϕ

(*g*t*), *pent*(*g*t*) (where *p* is the capture probability, which depends on the group (immatures, males and females) and assuming the animal is alive and in the study area, ϕ is the apparent survival, varying with the group and time, and *pent* is the probability of entry into the population per occasion *t* concerning *t-1*, and it depends on group and time). Model selection was performed using Akaike's information criterion corrected for small sample size (AICc) (Akaike 1973), and models differing by ≤2 ΔAICc were considered as potential alternatives (Burnham and Anderson 2002).

We used chi-square (χ^2) tests to compare sex ratios (observed and estimated frequencies of males and females) against an expected 1:1 ratio. To analyze differences in biometric variables across different size and sex groups, an ANOVA test is employed. The Kruskal-Wallis test was used to evaluate whether the survival rates for the size and sex groups were statistically significant. All statistical analyses were performed with R software (Development R Core Team 2017), with α set at 0.05 to evaluate statistical significance.

Results

During 2015–2016, 32 sampling campaigns were conducted, totaling approximately 60 hours of effort with an average survey yield of 2.55 captures/hour. During this period, 151 captures and recaptures were made, identifying 118 different individuals (Table 1). Adults comprised 73.73% (n=87) of the individuals in the studied population, with a sex ratio (♂♂/♂♂+♀♀) of 0.44 ($n_{♂♂}$=39; $n_{♀♀}$=48) that did not differ significantly from parity ($\chi^2_1 = 0.9310$, P = 0.3346), suggesting a relatively balanced distribution of males and females. In addition, 46.61% (n=55) of the captured individuals were found with tails that were not-intact (cut, regenerated, or in the process of regeneration). It is unclear whether the tailings were fully regenerated or are still in the process of regeneration, as this is not within the scope of the present study. Additionally, the limited number of recaptures has not yielded sufficient data to make a determination. A total of 21.85% (n=33) of the captures were recaptures. The percentage of recaptures by size class was as follows: juveniles, 4.55% (n=1); subadults, 9.09% (n=1); and adults, 26.27% (n=31). The proportion of recaptures by sex was 25.00% (n=13) for males and 27.27% (n=18) for females.

Table 1. Total captures (including recaptures) and individuals by age class and sex of *Anguis fragilis* from the population studied.

		Individuals		Captures	
		n	%	n	%
Juveniles		21	17.80	22	14.57
Subadults		10	8.47	11	7.28
Adults	Males	39	33.05	52	34.44
	Females	48	40.68	66	43.71
Total		**118**	**100.00**	**151**	**100.00**

The population exhibited a snout-vent length (SVL) of 149.50 mm (56.00, 204.00) (Table 2), without significant differences between adult males and adult females ($F_{(1,116)} = 0.0600$, P = 0.8021). The tail length (TL), excluding individuals with non-intact tails, was 163.09 mm (57.00, 249.00) (Table 2), also showing no significant differences between males and females ($F_{(1,45)} = 3.6831$, P = 0.0613). For weight, excluding individuals with amputated or regenerated tails and gravid females, the mean was 13.72 g (1.05, 32.30) (Table 2), with significant differences between the four size classes and sexes ($F_{(3,56)} = 69.0023$, P < 0.0001), but not between males and females (P = 0.6543).

Table 2. Biometric data of the size and sex classes considered. TotL: total length. SVL: snout-vent length. TL: tail length (from cloaca to end). All lengths are expressed in mm. Weight is expressed in grams. M: maximum. m: minimum. SD: standard deviation. *: Only individuals with the tail intact.

		n	Mean	m	M	SD
SVL	**Juveniles**	21	76.24	56.00	89.00	9.82
	Subadults	11	121.91	111.00	132.00	6.88
	Males	52	164.69	133.00	204.00	16.62
	Females	66	165.44	121.00	196.00	15.58
TL*	**Juveniles**	18	87.78	57.00	112.00	15.58
	Subadults	10	157.90	141.00	171.00	9.97
	Males	19	199.32	159.00	249.00	21.29
	Females	28	188.79	146.00	210.00	16.30
TotL*	**Juveniles**	18	163.67	113.00	202.00	26.01
	Subadults	10	280.60	252.00	303.00	15.90
	Males	19	359.16	296.00	414.00	32.74
	Females	28	348.36	267.00	393.00	32.71
Weight	**Juveniles**	18	2.50	1.05	5.00	1.09
	Subadults	10	9.16	6.36	12.24	1.98
	Males	19	22.32	10.34	32.30	5.66
	Females	13	20.19	9.23	29.34	6.86

Of the 151 captured individuals, 49.67% had their tails cut, regenerated, or regenerating. For size classes and sexes groups, they were 13.63% of juveniles, 10.00% of subadults, 57.14% of males, and 59.61% of females. The ratio (TL/TotL) obtained for all analyzed individuals was 0.56 ± 0,01 SD. Males have a slightly longer tail (TL) about the total length (TotL) than females (♂♂: 0.5544 ± 0.0147; ♀♀: 0.5425 ± 0.0115), with significant differences ($F_{(1,45)} = 9.6708$, P = 0.0032).

For the slow worm studied population, 16 possible models were tested to examine the influence of the variables considered on survival, including the interaction model including groups and time. The model focusing on Φ depending on time and sex was the most parsimonious, with a lower AICc value. The 15 remaining models were uncompetitive (>2.00 ΔAICc) (Table 3).

This model for the *A. fragilis* population considers the apparent survival (Φ) variable according to the group (males, females, or immatures) and over time, the probability of capture (*p*) variable with the group and constant over time, and the probability of entry to the population per occasion (*pent*) also remains variable by group and throughout the study period.

Table 3. Tested models in MARK, where p: capture probability; ϕ: apparent survival during the study period; pent: probability of entry into the population per occasion t; g: size class and sex groups (immatures, females, and males); and t: time. The selected model is in bold.

Model	AICc	ΔAICc	AICc Weights	Model Likelihood	Num. Par	Deviance	-2log(L)
{p(g*.), ϕ (g*t), pent(g*t)}	**-645.23**	**0.00**	**1.0000**	**1.0000**	**174**	**-186.8625**	**423.0466**
{p (.*t), ϕ (g*t), pent (g*t)}	-367.25	277.98	0.0281	0.0295	200	-211.9403	397.9688
{p(g*t), ϕ (g*t), pent(g*t)}	-190.27	454.96	0.0097	0.0099	258	-263.8636	346.0455
{p (g*.), ϕ (g*.), pent (g*t)}	2.03	647.26	0.0032	0.0033	1	0.0000	0.0000
{p (.*.), ϕ (.*.), pent (g*t)}	552.19	1197.42	0.0000	0.0000	20	-105.2897	504.6194
{p (g*t), ϕ (.*t), pent (g*t)}	662.81	1308.04	0.0000	0.0000	20	-105.2897	504.6194
{p (.*.), ϕ (g*t), pent (g*t)}	679.50	1324.73	0.0000	0.0000	70	-250.0525	359.8567
{p (g*t), ϕ (g*.), pent (g*t)}	710.19	1355.42	0.0000	0.0000	70	-250.0525	359.8567
{p (g*.), ϕ (.*.), pent (g*t)}	1102.23	1747.46	0.0000	0.0000	91	-108.2834	501.6257
{p (.*.), ϕ (g*.), pent (g*t)}	1102.23	1747.46	0.0000	0.0000	91	-108.2834	501.6257
{p (.*t), ϕ (g*.), pent (g*t)}	1755.50	2400.73	0.0000	0.0000	109	-162.4087	447.5004
{p (.*t), ϕ (g*.), pent (g*t)}	1755.50	2400.73	0.0000	0.0000	109	-162.4087	447.5004
{p (.*.), ϕ (.*t), pent (g*t)}	2118.43	2763.66	0.0000	0.0000	113	-148.8100	461.0991
{p (.*t), ϕ (.*t), pent (g*t)}	2497.37	3142.61	0.0000	0.0000	113	-148.8100	461.0991
{p (g*.), ϕ (.*t), pent (g*t)}	2851.29	3496.53	0.0000	0.0000	118	-154.9237	454.9854
{p (g*t), ϕ (.*.), pent (g*t)}	34698.98	35344.21	0.0000	0.0000	130	-230.9317	378.9774

The estimated apparent survival probabilities (Φ) during the study period (557 days or around 1.5 years) were variable according to the group (males, females, or immatures) and over time. The estimated mean apparent survival probability for the study period was 0.76 (0.54, 0.94) for immatures, 0.79 (0.29, 0.95) for males, and 0.83 (0.68, 0.96) for females (Table 4). No significant differences were found between size class and sexes groups ($H_{(2, 87)} = 3.4763$, $P = 0.1758$).

The probability of capture (p) variable with the group is constant over time. For immatures, it was 0.13 (0.05, 0.32), 0.15 (0.09, 0.24) for males, and 0.05 (0.03, 0.10) for females, without significant differences between size class and sexes groups.

The population size estimated (n) for the three classes considered was 46.69 ind. (22.56, 131.73) for immatures, 128.73 ind. (88.12, 210.46) for males, and 185.84 ind. (102.52, 376.79) for females (Table 4). The estimated sex ratio (♂♂/♂♂+♀♀) was 0.41, which significantly deviated from parity ($\chi^2_1 = 10.368$, $P = 0.0012$). The lower bound sex ratio of 0.36 ($\chi^2_1 = 1.0964$, $P = 0.2950$) is not significantly different from 0.5, while the upper bound sex ratio of 0.66 significantly deviates from parity ($\chi^2_1 = 47.0910$, $P < 0.0001$). The estimated density of population is 16.11 ind./ha (7.78, 45.42), 44.39 ind./ha (30.38, 72.57), and 64.08 ind./ha (35.35, 129.93) for immatures, males, and females, respectively.

The species' activity period extends from March to October, although isolated instances of activity have been observed as late as February. The species exhibits its highest level of activity between the months of May and June (Fig. 2). The males emerge from hibernation earlier than the females, with a peak in May. Female emergence occurs one month later, with a peak in June (Fig. 3). The activity patterns of juveniles and subadults were found to be more similar to those of females for the former and to those of males for the latter (Fig. 3). The species' activity is significantly diminished during the summer months, with males exhibiting almost no activity at all. Female, juvenile, and subadult individuals exhibit minimal activity from the end of summer until the month of October (Fig. 3).

A total of 41.18% of captured males exhibited recent scars and wounds, indicative of fighting during the mating season from mid-April to mid-June, with the majority (61.90%) of these injuries occurring in May (Fig. 4). Of the 66 females captured, 41 (62.12%) were pregnant. In 2015, this percentage was 60.87% (n=28), while in 2016 it was 65.00% (n=13). Pregnant females were observed between mid-May and early September, with the greatest incidence occurring in June (69.79%). During the period from May to August, 78.48% of the females were pregnant (Fig. 4). No gravid females were found with a snout-vent length (SVL) of less than 149 mm. Regarding female size, 100% of females with an SVL greater than 180 mm were pregnant between May and July, compared to only 69.40% of females of smaller sizes.

Table 4. Estimated population and survival parameters for three groups of *Anguis fragilis* population. SE: Standard error. CI: confidence interval. Φ: survival rate.

Group	Population size				Survival estimators			
	n	SE	95% Lower CI bound	95% Upper CI bound	ϕ	SE	95% Lower CI bound	95% Upper CI bound
Immatures	46.69	24.09	22.56	131.73	0.7522	0.0602	0.6287	0.8758
Males	128.73	29.74	88.12	210.46	0.7803	0.0615	0.6541	0.9965
Females	185.84	65.46	102.52	376.79	0.8335	0.0644	0.6913	0.9557

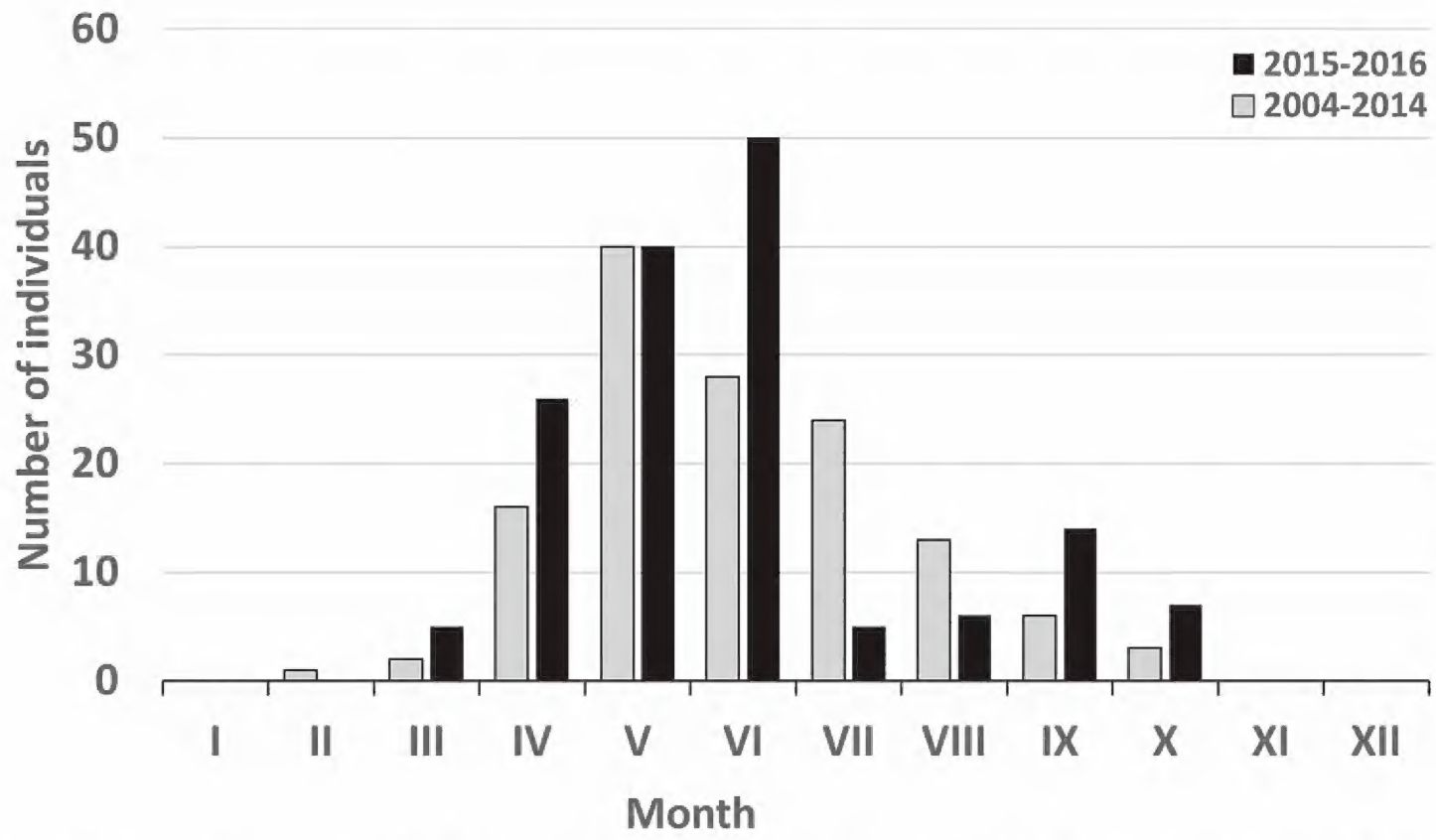

Figure 2. Capture frequency by month during the study period (2015–2016) and during sporadic sampling from 2004–2014 (J. Roig and G. Giner in SARE monitoring, Montori et al. 2014).

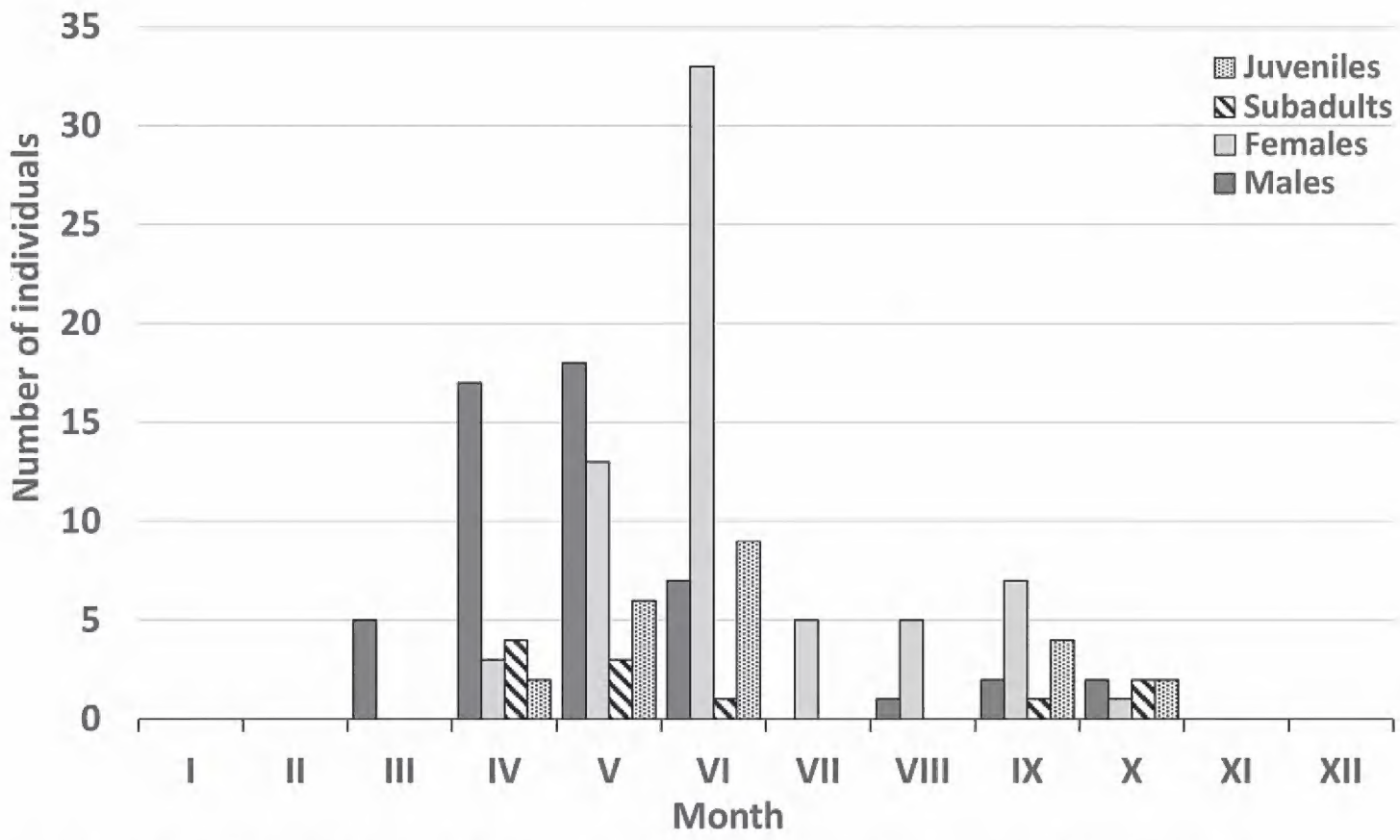

Figure 3. Frequency of monthly captures by size, class, and sex during the present study (2015–2016).

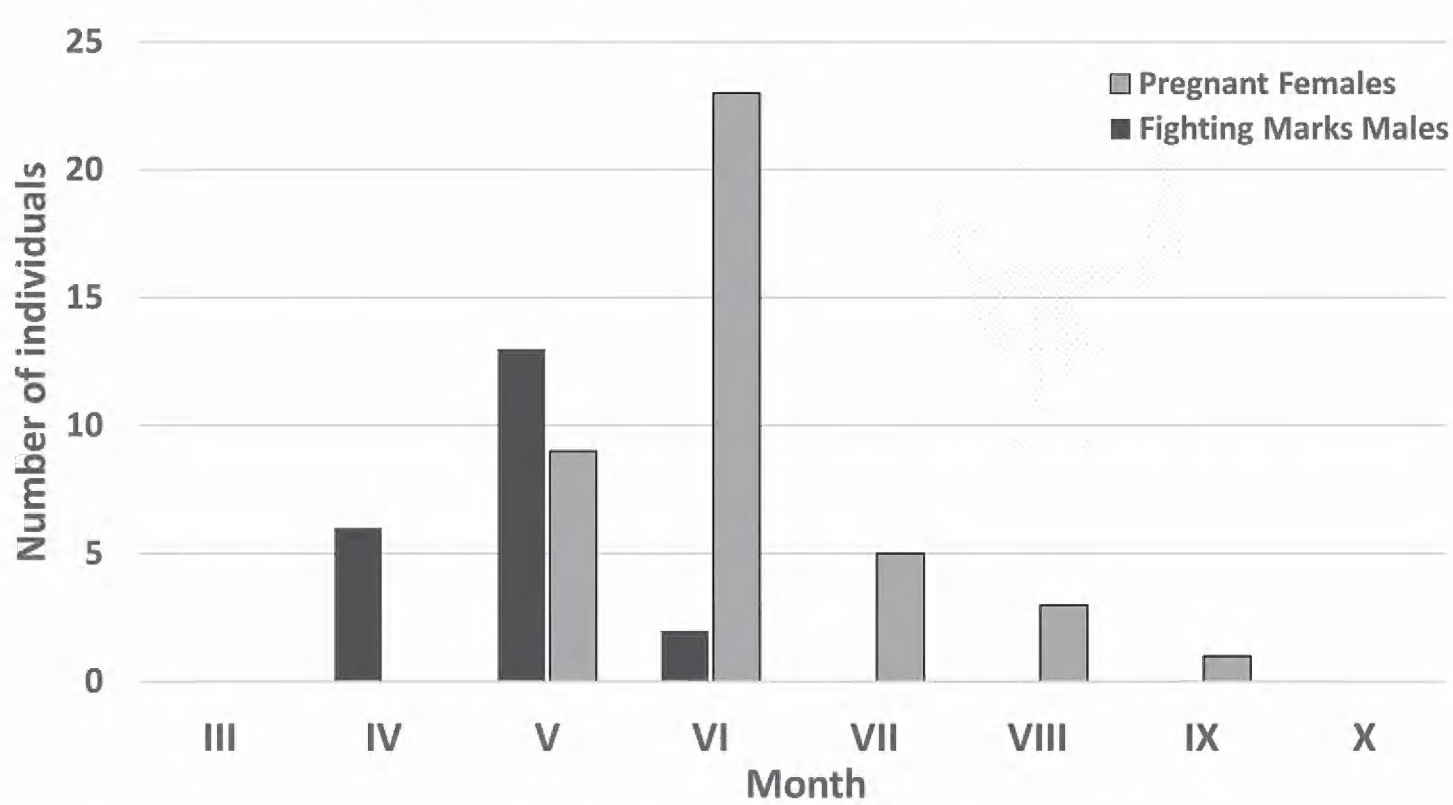

Figure 4. Monthly distribution of recently combat-marked males and pregnant females (2015–2016).

Discussion

Adults constitute 89.58% of the population, indicating either a low number or low detectability of subadults. Additionally, the low catchability of juveniles has prevented the collection of sufficient data on this age class.

Dely (1981) reports a maximum snout-vent length (SVL) of 291 mm and a maximum tail length (TL) of 280 mm for the species. The maximum sizes obtained in the present study (204 mm SVL and 249 mm TL) are smaller but within the described ranges for the species (Table 5). Males in this population tend to be slightly longer and heavier than females, although the differences are not significant. There is considerable variability in the average lengths of individuals across different populations, with either males or females reaching greater lengths depending on the study (Table 5), which often vary in time, season, and sampling methodology.

Most studies have not focused on collecting biometric parameters, resulting in limited data on the species' biometry across different populations, often based on small sample sizes (Galán 2003). While most studies report the maximum and minimum lengths of the specimens found, the average total lengths of adults are practically non-existent. Additionally, averages are often calculated together with the entire juvenile and subadult population (Welsch and Schlüpmann 2022), leading to a general lack of detailed information. Smith (1990) attempted to estimate the maximum lengths of males and females in his studied populations using various statistical methods to compare sexes, but these were not definitive in establishing actual lengths (Table 5).

In specimens with complete tails, the tail length (TL) was always greater than the snout-vent length (SVL). The TL/SVL ratios were as follows: males (average = 1.25, SD = 0.08) and females (average = 1.18, SD = 0.05). Dely (1981) reports a ratio of 1.02–1.36, Malkmus (1987) of 1.05–1.26, Vences (1993) of 1.27 on average, and Blosat (1997) of 1.19 on average. Ratios below 1 are indicative of tail autotomy. The percentage of individuals with broken or regenerated tails is similar to other studies, at around 50% of adult specimens (Stumpel 1985; Smith 1990; Blosat 1997; Ferreiro and Galán 2004). There is no significant difference between sexes in the incidence of broken tails, with males and females showing similar percentages (males: 59.61%; females: 57.14%), although the incidence is slightly higher in males. As observed in other populations (Welsch and Schlüpmann 2017), 100% of large individuals have regenerated or cut tails. In our population, this occurs in males with SVL greater than 180 mm, while in females, 100% of regenerated or cut tails are observed at 190 mm SVL.

In males, tail injuries are often interpreted as resulting from combat behavior between males during the mating period or from antipredator encounters. Capula et al. (1998) found that, in an alpine *A. fragilis* (*sensu lato*) population, males defeated in combats were always smaller than the victors, similar to other reptile species (e.g., Luiselli 1993). The mean length of males courting and successfully mating with females was significantly greater than the mean length of males in the study area. As suggested by Capula et al. (1998), access to reproductive females is likely monopolized by the larger males in the population. During mating, males bite females (usually on the head or neck) and try to align their vents, apparently forcing copulation. This could explain the high number of cut or regenerated tails found in females.

The population estimation results indicate an average density of 120.57 individuals per hectare (16.10 immatures/juveniles, 44.39 females, and 60.08 males), resulting in an estimated mean population of 349.65 individuals in our study area. Capula et al. (1998) reported densities higher than 80 individuals per hectare. Vences (1993) estimated a total population of 150 individuals in an isolated area of 1500 m², corresponding to a density of 1000 individuals per hectare. Hubble and Hurst (2006) captured 577 individuals in 2.5 hectares, representing 230.8 individuals per hectare. These values are higher than those obtained in the present study but are much lower than those reported by Ferreiro and Galán (2002), who estimated a density of 1700 individuals per hectare in the Visma population (Coruña A, Spain) using mark-capture-recapture methodology.

Table 5. Biometric data for different countries and regions in the natural populations of the species. TotL: average of total length. SVL: average of snout-vent length. TL: average of tail length. Lengths in mm. Weight in grams. MM: males, and FF: females.

Region (Country)	TotL		SVL		TL		Weight		References
	MM	FF	MM	FF	MM	FF	MM	FF	
Asturias (ES)			168.00	160.00					Braña (1983)
Utrecht (NL)	282.10	330.20	142.70	156.40			8.50	19.40	Stumpel (1995)
Dorset (UK)			151.70–156.30	153.50–157.70					Smith (1990)
Coruña A (ES)			151.00	154.00					Vences (1993)
Islas Cíes (ES)			151.00	170.00	192.20	236.30	17.00	20.20	Galán (2003)
Coruña A (ES)			172.00	153.00					Cabido (2004)
Galicia (ES)				168.30	183.90	184.00		13.76	Ferreiro and Galán (2004)
Coruña A (ES)			159.8	156.4					Ferreiro et al. (2007)
North Rhine (Westfalia)	308.60	334.20	143.60	158.60	171.60	185.10	16.30	22.40	Blosat (1997)
North Rhine (Westfalia)	293.00	291.00	173.00	166.00	120.00	125.00	22.30	20.30	Schlüpmann (2020)
Westfalia (D)			131.00						Welsch and Schlüpmann (2022)
Tarragona (ES)	358.40	344.80	165.10	162.90	198.90	187.40	22.05	19.31	Present study (2015–2016)

In the study area, the species begins to be active at the end of February or the beginning of March and remains active until the end of October, with activity potentially extending into November in years with favorable weather conditions. This activity period aligns with that described for many European populations inhabiting temperate areas or low altitudes, such as in Coruña A (Ferreiro and Galán 2004). In these areas, individuals maintain a much longer period of activity. Males can be active from early February until mid-October, with peak activity from March to June, while females are active from mid-March until mid-December, with peak activity from May to August. Subadults are active from February until mid-December, with peak activity in May and June. In contrast, populations at higher altitudes or latitudes, where temperatures are colder, have a reduced activity period. For instance, in the Italian Alps (Tarvisio Forest, Capula et al. 1998), activity starts after the snow melts, usually in mid-April. In southern England, activity may be delayed until May or June (Smith 1990; Platenberg 1999). However, in more temperate regions such as North Rhine-Westphalia, Germany, activity starts at the end of February and ends in early October (Schlüpmann 2020).

The reproductive period for males in the study area is estimated to start approximately two to three weeks after they emerge from their winter shelters, in early April. From then until the end of June (the end of the mating season for males in the area), males have been found with recent wounds and scars, typically matching the shape and size of the mouth of *A. fragilis*. This method of assessing recent wounds is effective for determining the reproductive period of males in this species. The period of male combat starts earlier in our population compared to Alpine populations (May, Capula et al. 1998) in northeastern Italy. Despite similar altitudes (990 m and 1100 m), the greater influence of the Mediterranean climate on our population may explain this earlier onset of male-male combat. Male-male combats occur earlier than copulations (Fig. 4), but both fighting and copulation behaviors peak in May, as described by Capula et al. (2008). These authors indicate that this peak coincides with the maximum of copulations. In our study, we did not observe copulations directly but noted a peak in the presence of pregnant females in June (Fig. 4).

The reproductive pattern of *A. fragilis*, with 62.12% of females being gravid, is consistent with findings from other European studies, indicating that not all females breed annually. In southern England, gravid rates ranged from 55% to 70%, indicating that a significant proportion of females may skip reproduction each year (Reading 1997). Such variability may be influenced by several ecological and physiological factors, including the availability of resources, health status, and age (Platenberg 1999). Similar trends are observed in Germany, with annual pregnancy rates varying between 50% and 65% due to environmental conditions (Strijbosch et al. 1989). In the Czech Republic, approximately 60% of females were found to be gravid, thereby confirming that while *A. fragilis* is capable of adapting to a variety of habitats, not all females reproduce each season (Gvoždík et al. 2007). This strategy may confer an evolutionary advantage by allowing females to prioritize growth and survival in unfavorable conditions, thereby enhancing long-term reproductive success.

Females were observed in a clear state of gestation between April and September. Many of them exhibited various wounds and excoriations on the scales of the cervical area, caused by male bites during copulation. These marks were much lighter than those resulting from fights between males. The presence of these marks, along with the ventral palpation of suspected gravid females, was decisive in most cases where pregnancy was not visually apparent. However, some females with breeding bites did not show signs of pregnancy upon subsequent recapture. This may suggest that sperm storage occurs in *A. fragilis*, as observed in lacertids, with evidence of sperm storage in *Acanthodactylus schreiberi* (Zotos et al. 2012). The role of stored sperm in determining breeding dates in female sand lizards (*Lacerta agilis*) has been documented, indicating the importance of this mechanism in reptilian reproductive strategies (Olsson et al. 1997). In the study area, gravid females are found from May to September (Fig. 5), which is a particularly long period. In Coruña A (Ferreiro and Galán 2004; Ferreiro et al. 2007), gravid females were found from mid-July to early August, a shorter time interval compared to our population.

The smallest female observed in the field showing evidence of being pregnant was 149 mm SVL, a size that coincides with findings by Capula et al. (1992) in Italy NE and by Alfermann and Völkl (2004) in Augsburg, Germany. However, this is considerably larger than the 120–129 mm size class in which Patterson (1983) found pregnant females on the island of Portland in southern Great Britain. In the Northwestern Iberian Peninsula, the minimum size of pregnant females found was 137.0 mm in Asturias (Braña 1983) and 135 mm in Coruña A (Ferreiro and Galán 2004). Ferreiro and Galán (2004) suggest that the minimum maturity size of slow worm females varies between 135 and 150 mm.

In the study area, the reproductive cycle extends from March to September, closely aligning with the findings of other researchers (Braña 1983; Ferreiro and Galán 2004). The percentage of gravid females in our population (Fig. 5) is high compared to other populations. This data indicates that most females are gravid each year, in contrast to the results obtained in northern Europe (Patterson 1983; Stumpel 1985; Smith 1990) or in alpine populations (Capula et al. 1992, 1998), where gestation is predominantly biennial. In Asturias, Braña (1983) reports a percentage of 65% of gravid females during the reproductive period. In Coruña A, 88.8% of the females reproduce annually, likely due to the temperate and humid coastal climate (Ferreiro and Galán 2004). However, in the Netherlands, the percentage of gravid females varies between 31% and 81% in different years (Stumpel 1985).

Several hypotheses are proposed to explain these variations. One suggests that only gravid females engage in superficial thermoregulatory activity in warm

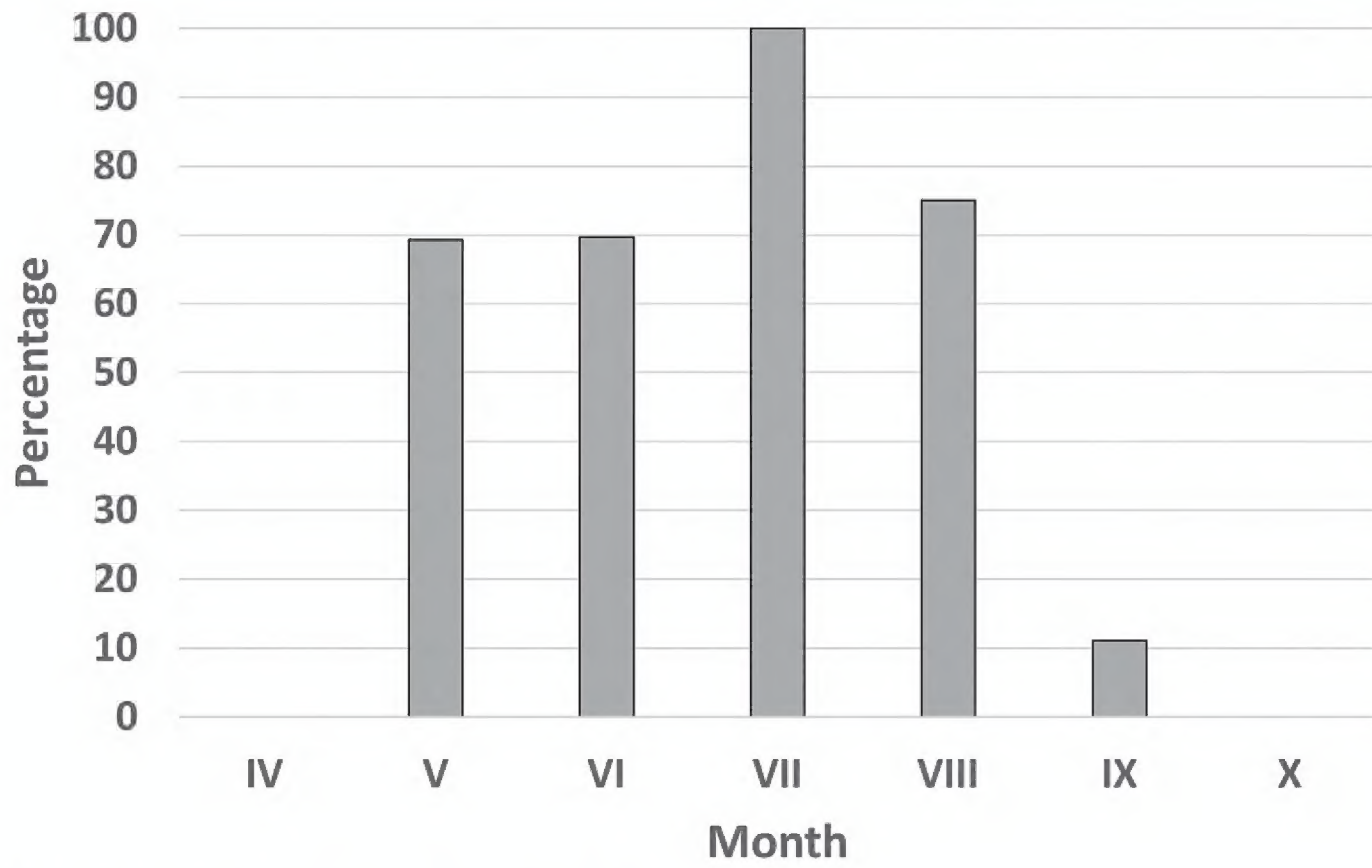

Figure 5. Percentage of gravid females found throughout the year (n=41).

environments, as observed in our population (Patterson 1983; Platenberg 1999; Graitson 2003), while non-gravid females remain active in deeper, cooler, and more humid areas. Another hypothesis posits that the high Mediterranean nature of the population allows all females to accumulate sufficient reserves during the activity period to reproduce annually. Under this assumption, annual or biennial reproduction could depend on climatic conditions or the abundance of trophic resources rather than following a fixed pattern. Further studies are required to validate these hypotheses.

Throughout July and August, soil moisture decreases and temperatures increase in the study area, resulting in fewer encounters under the surveyed shelters. Meek (2005) demonstrates that the species continues underground activity if the surrounding substrate temperature is within its preferred range, thus reducing the need to bask and seek warmth. This behavior is of particular importance during the warmer months, as very few individuals are detected in the shelters, with gravid females representing the exception. Similarly, Riddell (1996) observed a comparable pattern during an especially hot and dry summer in his study area, noting the presence of only a few individuals. Graitson (2004) obtained analogous results. This evidence suggests an interaction between thermoregulation and hydroregulation, with a potential shift in priorities among pregnant females (Gregory 1980). Patterson (1983) states that drought conditions hinder foraging for food, such as slugs and worms, preventing many females from fully recovering from the energy investment of previous pregnancies. This is one reason why the species exhibits biennial reproduction in females, due to the limited optimal feeding time available to some populations. However, in Hampshire, UK, peak activity occurs in late August and early September due to the milder and more humid climate.

Low numbers of juveniles (SVL<100 mm) were observed throughout the study period, with none detected in July and August. This absence is likely due to high temperatures and low humidity conditions, which force juveniles to seek deeper shelters to avoid dehydration (Sannolo and Carretero 2019). Similar results were obtained by Graitson (2004) in Belgium, where mainly gravid females were found during the summer period. No reliable evidence was found for the timing of parturition and recruitment. Hatchling size has been shown to be directly proportional to maternal size (Ferreiro and Galán 2004), making it difficult to determine with certainty whether the smallest juveniles found were hatchlings. The smallest juveniles found were two specimens measuring 56 mm, likely considered neonates, located in mid-September and late October, respectively. This suggests a normal calving period for the species, although it is longer in the studied area than in other European populations. Ferreiro and Galán (2004) suggest that, in years with milder weather, this gestation period is reduced. The normal breeding period in England is between mid-August and mid-September (Beebee and Griffiths 2000), similar to Galicia (Ferreiro and Galán 2004).

The sex ratio fluctuates significantly throughout the year, which is common for the species according to other long-term studies (Smith 1990; Ferreiro and Galán 2004; Thiesmeier et al. 2013). Males are typically found first in spring, followed by an increase in females throughout the year, while males almost completely disappear in summer. The sex ratio can vary greatly between populations. For instance, some populations have a higher proportion of males (♂♂/total): 0.6 in two populations in Coruña A and 0.65 in Dorset (Smith 1990; Vences 1993; Ferreiro and Galán 2004). In contrast, many populations have a female-biased sex ratio, as observed in our study, with values such as 0.22 in Utrecht, 0.38 in Dorset, 0.30 in Hampshire, 0.35 in two populations in Germany, and 0.10 in Ireland (Stumpel 1985; Smith 1990; Greven et al. 2006; Hubble and Hurst 2006; Thiesmeier et al. 2013; Parry 2020). The sex ratio of the studied population (♂♂/total = 0.44) suggests a slightly higher proportion of females compared to males, although this difference was

not statistically significant and remains balanced between both sexes, fitting within the species' variability. Studies based on short-term monitoring (Stumpel 1985) or visual detection of active individuals (Parry 2020) may present a biased view of sex ratios.

A very low number of subadults was detected in the studied population. In long-lived species such as the Slow Worm, it is typical for the number of adults to be much higher than the number of juveniles (Beebee and Griffiths 2000). However, other studies (Riddell 1996; Hubble and Hurst 2006; Thiesmeier 2013) have reported populations with a much higher percentage of both subadults and juveniles. For instance, in Petersfield, UK, 310 immatures (51.7%) were recorded compared to 267 adults. In our population, both juveniles and subadults were detected in low percentages, with no significant differences in their capture rates throughout the monitoring period. This could indicate a very low turnover rate, but consistent with previous research, it may also be due to the need for more appropriate methodologies, such as installing artificial refuges (Hubble and Hurst 2006). The presence of other refuges, such as ground cracks, which are more suitable for juveniles, likely hinders their detection and is the most probable cause of this underestimation.

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